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Abstract

Sexual size dimorphism occurs throughout the animal kingdom, and its ecological and evolutionary causes and implications have been intensively studied. Sex-specific differences in bill curvature are known in several species of birds, including some tropical hummingbirds. Despite the importance of bill shape for foraging, comparative studies of sexual dimorphism of bill shape are few. We quantified bill shape in two temperate hummingbird species, Black-chinned Hummingbird (*Archilochus alexandri*) and Ruby-throated Hummingbird (*A. colubris*) and compared patterns of sexual shape dimorphism. Several commonly used bill-curvature indices yielded contrasting results; one found differences between species and sexes, a second identified no differences in curvature, and a circle-curvature approach revealed shape differences between species and between the sexes. By contrast, landmark-based geometric morphometric methods identified significant differences in sexual shape dimorphism and also revealed that Ruby-throated Hummingbirds exhibited significant sexual differences in shape, whereas Black-chinned Hummingbirds did not. Female Ruby-throated Hummingbirds exhibited relatively greater bill curvature than males, a pattern consistent with observations of some tropical hummingbirds. Although the causes of differences in bill-shape dimorphism between Black-chinned and Ruby-throated hummingbirds remain unclear, we hypothesize that it may be attributable to differences in the structure of the community in which each species breeds and the interplay between inter- and intraspecific competition for resources in these communities. Finally, we recommend that future studies of bill shape include geometric morphometric approaches because they are better suited than univariate approaches for identifying more complex shape differences within and among species.

Keywords

Archilochus alexandri, *A. colubris*, bill morphology, Black-chinned Hummingbird, geometric morphometrics, Ruby-throated Hummingbird, sexual dimorphism, Trochilidae

Disciplines

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BILL SHAPE AND SEXUAL SHAPE DIMORPHISM BETWEEN TWO SPECIES OF TEMPERATE HUMMINGBIRDS: BLACK-CHINNED HUMMINGBIRD (*ARCHILOCHUS ALEXANDRI*) AND RUBY-THROATED HUMMINGBIRD (*A. COLUBRIS*)

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ABSTRACT.—Sexual size dimorphism occurs throughout the animal kingdom, and its ecological and evolutionary causes and implications have been intensively studied. Sex-specific differences in bill curvature are known in several species of birds, including some tropical hummingbirds. Despite the importance of bill shape for foraging, comparative studies of sexual dimorphism of bill shape are few. We quantified bill shape in two temperate hummingbird species, Black-chinned Hummingbird (*Archilocus alexandri*) and Ruby-throated Hummingbird (*A. colubris*) and compared patterns of sexual shape dimorphism. Several commonly used bill-curvature indices yielded contrasting results; one found differences between species and sexes, a second identified no differences in curvature, and a circle-curvature approach revealed shape differences between species and between the sexes. By contrast, landmark-based geometric morphometric methods identified significant differences in sexual shape dimorphism and also revealed that Ruby-throated Hummingbirds exhibited significant sexual differences in shape, whereas Black-chinned Hummingbirds did not. Female Ruby-throated Hummingbirds exhibited relatively greater bill curvature than males, a pattern consistent with observations of some tropical hummingbirds. Although the causes of differences in bill-shape dimorphism between Black-chinned and Ruby-throated hummingbirds remain unclear, we hypothesize that it may be attributable to differences in the structure of the community in which each species breeds and the interplay between inter- and intraspecific competition for resources in these communities. Finally, we recommend that future studies of bill shape include geometric morphometric approaches because they are better suited than univariate approaches for identifying more complex shape differences within and among species. *Received 26 October 2009, accepted 10 March 2010.*

Key words: *Archilocus alexandri*, *A. colubris*, bill morphology, Black-chinned Hummingbird, geometric morphometrics, Ruby-throated Hummingbird, sexual dimorphism, Trochilidae.

Formal del Pico y Dimorfismo Sexual entre Dos Especies de Picaflores de la Zona Templada: *Archilochus alexandri* y *A. colubris*

RESUMEN.—El dimorfismo sexual en el tamaño se presenta a través del reino animal, y sus causas e implicancias ecológicas y evolutivas han sido intensamente estudiadas. Las diferencias específicas de los sexos en la curvatura del pico son conocidas en varias especies de aves, incluyendo algunos picaflores tropicales. A pesar de la importancia de la forma del pico para forrajear, los estudios comparativos de dimorfismo sexual en la forma del pico son escasos. Cuantificamos la forma del pico en dos especies de picaflores de la zona templada, *Archilocus alexandri* y *A. colubris*, y comparamos los patrones de dimorfismo sexual en la forma. Varios índices de curvatura del pico comúnmente usados arrojaron resultados contrastantes: uno encontró diferencias entre especies y sexos, otro no identificó diferencias en la curvatura y un enfoque de círculo-curvatura reveló diferencias en la forma entre especies y entre los sexos. En contraste, los métodos de morfometría geométrica basados en puntos de referencia identificaron diferencias significativas en el dimorfismo sexual en la forma y también revelaron que *A. colubris* exhibió diferencias sexuales significativas en la forma, mientras que *A. alexandri* no. Las hembras de *A. colubris* exhibieron curvaturas de los picos relativamente mayores que los machos, un patrón que concuerda con observaciones de algunos picaflores tropicales. Aunque las causas de las diferencias en el dimorfismo en la forma del pico entre *A. alexandri* y *A. colubris* permanecen poco claras, hipotetizamos que podrían ser atribuibles a diferencias en la estructura de la comunidad en la cual cada especie cría y a la interacción entre competencia inter- e intra-específica por los recursos en estas comunidades. Finalmente, recomendamos que los estudios futuros de la forma del pico incluyan enfoques de morfometría geométrica debido a que son más adecuados que los enfoques univariados para identificar diferencias más complejas en la forma dentro de especies y entre especies.

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SEXUAL DIMORPHISM is found throughout the animal kingdom, and its consequences for the ecology and evolution of organisms are often profound. One pattern frequently observed is sexual size dimorphism (SSD), and a number of mechanisms have been proposed to explain its variable distribution among taxa (Abouheif and Fairbairn 1997, Colwell 2000). Darwin (1871) proposed that sexual selection and selection for increased fecundity could be mechanisms that explain patterns of size dimorphism (see also Møller 1988, Andersson 1994). Other hypotheses suggest that sexual dimorphism evolves from competition over resources between the sexes (Selander 1972) or because of sex-specific responses to environmental gradients (Hendry et al. 2006). In some species, sexual dimorphism may be driven by differences in the reproductive roles of males and females (Ralls 1976). When these processes occur in closely related species, distinct patterns of size dimorphism among species can result (Rensch 1960, Dale et al. 2007).

In addition to body size, males and females may also differ widely in shape (Hendry et al. 2006, Butler et al. 2007). Curiously, although shape contributes meaningfully to various ecological functions, such as feeding, mating, parental care, and other life-history characteristics, sexual shape dimorphism has received considerably less attention than sexual size differences (Lande and Arnold 1985, Hedrick and Temeles 1989, Gidaszewski et al. 2009). Sexual shape dimorphism has been identified in numerous taxa, including dipterans (Bonduriansky 2007), fish (Hendry et al. 2006), turtles (Valenzuela et al. 2004), and lizards (Butler et al. 2007), to name a few. In those cases that have been studied, both natural and sexual selection have contributed to the evolution of shape differences between the sexes (Hendry et al. 2006, Butler et al. 2007).

Hummingbirds are an ideal system for the study of sexual shape dimorphism. This diverse group of New World birds represents a monophyletic lineage (family Trochilidae) of 331 currently recognized species (McGuire et al. 2007). Both intraspecific and interspecific competition are prevalent in hummingbirds, both within and between the sexes (Kodric-Brown and Brown 1978). Females perform all parental care (Kaufman 1996), and migratory hummingbirds exhibit sexual differences in the pattern and timing of migration. Sexual dimorphism occurs in a number of characteristics, such as wing morphology (Stiles et al. 2005) and, in some cases, bill morphology. Although many anatomical attributes contribute to successful foraging in hummingbirds, bill morphology is a critical trait that is likely under strong selection (Colwell 2000) and is tightly linked with feeding efficiency and foraging preferences in many species (Gould 1861, Darwin 1871). Bill morphology affects niche differentiation both among species and between the sexes (e.g., Feinsinger and Colwell 1978). Considerable research has examined the functional relationship between hummingbird bill morphology and a species' food resource niche, particularly in tropical species (Snow and Snow 1972, Wolf et al. 1976, Feinsinger and Colwell 1978, Temeles and Roberts 1993, Altshuler and Clark 2003). Additionally, in some species, differences in bill size and bill curvature between the sexes are associated with differences in foraging (Paton and Collins 1989; Carpenter et al. 1991; Temeles et al. 2000, 2005, 2009). Hummingbirds also feed on arthropods, but foraging niches and bill morphology appear to be more related to nectivory (Stiles 1995). For example, the bills of female Purple-throated Caribs (*Eulampis jugularis*) are longer and more curved than the bills of males, and these bill differences

correspond to morphological differences in the flowers (*Heliconia* spp.) that each sex primarily feeds on (Temeles et al. 2000, Temeles and Kress 2003).

Previous descriptions of hummingbird bill morphology have used univariate indices that were derived mainly from the ratios of linear measurements. One approach estimates bill curvature from measurements on the maxilla, whereas another estimates bill curvature from measurements of the mandible (e.g., Paton and Collins 1989, Stiles 1995). In addition, a recent approach used the mathematical definition of curvature to quantify bill shape (Temeles et al. 2009). Although these methods provide simple and intuitive estimates of bill shape and curvature, several shortcomings may limit their utility for comparative studies across species. For instance, with the first two indices, it is possible that bills with different shapes can yield identical values, because the locations of the measurements on the bill are not recorded. For example, if maximum bill depth is nearer to the bill tip in one species and nearer to the base of the bill in another species, the ratio of length to depth could be the same for two species with different bill shapes (for a similar discussion, see Adams et al. 2004). Additionally, the third index assumes that bill curvature is constant across the length of the bill, because the approach is derived from the mathematical definition of curvature based on a circle. Although bill curvature may be relatively constant in some species (e.g., Purple-throated Carib), in others the curvature is greater either toward the tip (e.g., White-necked Jacobin [*Florisuga mellivora*]) or the base of the bill (e.g., Sword-billed Hummingbird [*Ensifera ensifera*]). In these cases, comparative studies among species may be compromised if univariate indices are used to quantify bill shape.

By contrast, landmark-based geometric morphometric methods (Rohlf and Marcus 1993, Adams et al. 2004) do not suffer from these shortcomings. These methods allow a rigorous quantification of shape from the locations of anatomical coordinates, after the effects of nonshape variation have been mathematically held constant. Landmark-based morphometric methods are commonly used in evolutionary biology and anthropology to quantify shape differences in a wide variety of organisms (e.g., Adams and Rohlf 2000, Koecher et al. 2002, Kassam et al. 2003, Langerhans and DeWitt 2004, Taylor et al. 2006, Butterworth et al. 2009), including birds (e.g., Foster et al. 2008, Kulemeyer et al. 2009, Navarro et al. 2009).

Two sister taxa of temperate-zone-breeding, migratory species, the Black-chinned Hummingbird (*Archilochus alexandri*) and the Ruby-throated Hummingbird (*A. colubris*), present an opportunity to compare bill shape across closely related taxa. The Black-chinned Hummingbird is a generalized and adaptable species (Baltosser and Russell 2000) whose breeding range overlaps that of several other species of hummingbirds in western North America (Ewald and Bransfield 1987). The Ruby-throated Hummingbird, on the other hand, is the only species of hummingbird that breeds in eastern North America (Robinson et al. 1996). Breeding territories of male and female Black-chinned Hummingbirds are found in different habitats (e.g., Stiles 1973, Baltosser 1989), whereas both sexes of the Ruby-throated Hummingbird share the same habitat. Finally, bill morphology in Ruby-throated Hummingbirds appears to be related to foraging and is correlated with flower morphology (Bertin 1982). Viewing these patterns in light of what is known of tropical hummingbirds suggests the hypothesis that bill morphology in these species may be shaped by

foraging behavior and that morphological patterns of bill shape may differ between the sexes. To date, however, this hypothesis has not been formally tested.

We examined patterns of bill shape in Black-chinned and Ruby-throated hummingbirds to quantify interspecific differences in bill morphology as well as patterns of sexual shape dimorphism. From previous ecological work, we hypothesized that Ruby-throated Hummingbirds would exhibit greater sexual shape dimorphism than Black-chinned Hummingbirds. We tested this hypothesis using bill shape quantified by the three curvature indices described above as well as by landmark-based geometric morphometric methods. In addition, we explicitly addressed the suggestion of Temeles and Kress (2003) that, although some hummingbirds have less extreme sexual size differences, they may still exhibit other sexual differences in bill morphology. If such patterns are identified, they suggest that foraging ecology plays a greater role in contributing to sexual differences across taxa than was previously appreciated.

METHODS

Specimen information.—We obtained 286 adult Black-chinned Hummingbirds (160 females and 126 males) and 78 Ruby-throated Hummingbirds (35 females and 43 males) that were collected between 15 May and 15 August (see Appendix). The specimens were divided into geographic localities that corresponded to breeding populations. Our data thus consisted of Black-chinned Hummingbirds from two localities (Arizona and California) and Ruby-throated Hummingbirds from three localities (Michigan, New York, and Pennsylvania).

Morphometrics.—Bill shape of all specimens was measured using several approaches. First, we used three indices designed to capture overall bill curvature. One index estimates bill curvature by calculating the arc:chord ratio as the linear measurement of the exposed culmen (chord) to the curvilinear measurement (arc) taken across the maxilla (Stiles 1995; Fig. 1A). A second index measures curvature of the mandible as depth:length ratio from the linear distance of the mandible to gape (length) to the maximum distance between this measurement and the edge of the upper mandible (height/gape, *sensu* Paton and Collins 1989, Collins 2008; Fig. 1B). The third index estimates bill curvature from the angle of declination of the bill in relation to the horizontal plane, using the mathematical definition of curvature as based on a circle (see Temeles et al. 2009; Fig. 1C). Finally, we used landmark-based geometric morphometric methods to quantify bill shape. First, digital images of the left-lateral side of the head and bill of each specimen were taken using a Nikon DXM-1200 digital camera mounted on a Nikon SMZ 1500 stereomicroscope. We then recorded the locations of 10 biologically homologous landmarks and 15 sliding semi-landmarks, which together were chosen to represent the shape and outline of the bill (Fig. 1D) using the program TPSDIG2 (Rohlf 2006). Nonshape variation was removed using a generalized Procrustes analysis that superimposed specimens onto a common coordinate system after accounting for differences in position, orientation, and scale (Rohlf and Slice 1990). During this procedure, semi-landmarks were permitted to slide along the outline of the bill to minimize shape differences (e.g., Bookstein et al. 1999). From the aligned specimens, shape variables were then

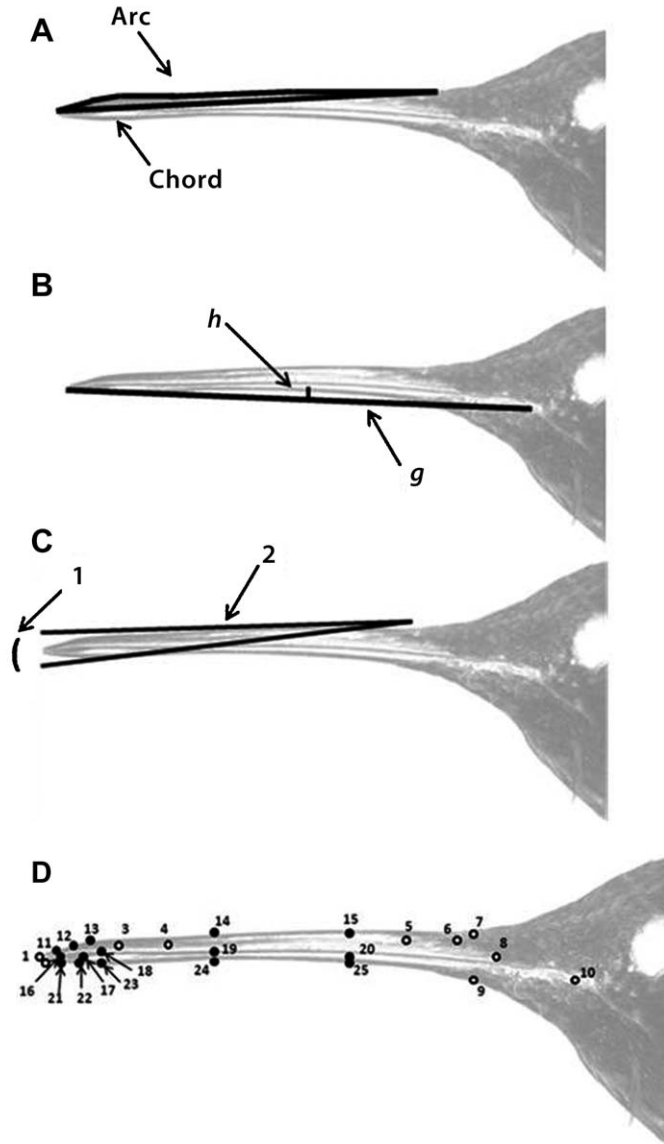


FIG. 1. Curvature indices and landmark-based morphometrics, shown on a Black-chinned Hummingbird. (A) Measurements of the maxillary curvature index (arc:chord ratio). (B) Mandibular curvature index, where h is the maximum height of the edge of the upper mandible to g (bill tip to gape). (C) Circle-curvature method, where 1 is the angle and 2 is chord length. (D) Landmark-based geometric morphometrics. Open circles designate landmarks, and filled circles represent sliding semi-landmarks.

generated using the thin-plate spline (Bookstein 1991) and standard uniform components (Rohlf and Bookstein 2003). Because the number of shape variables (46) was greater than the number of dimensions of actual shape information (due to the additional standardization of the semi-landmarks), we performed a principal component analysis (PCA) of shape and retained only the dimensions that contained variation. These 35 variables were then used in all subsequent analyses to represent bill shape. These procedures were performed in TPSRELW (Rohlf 2007).

Statistical analyses.—We used analysis of variance (ANOVA) to examine variation in bill morphology. A factorial ANOVA was performed on each curvature index, with species and sex as main effects, and included a species*sex interaction term. For the landmark-based shape variables we used a factorial multivariate analysis of variance (MANOVA), with the same effects (species, sex, and species*sex interaction), to determine whether species exhibited differences in bill shape and whether sexual shape dimorphism existed. We then determined whether patterns of sexual shape dimorphism were concordant across species, by comparing the observed morphological differentiation between male and female Ruby-throated Hummingbirds with that exhibited in Black-chinned Hummingbirds.

For the landmark-based shape variables, the observed sexual shape dimorphism of each species was expressed as a multivariate vector that connected the phenotypic means of males and females (see Adams and Collyer 2009). Differences in the magnitude of these vectors were considered a measure of the difference in sexual shape dimorphism between species. We calculated sexual-shape-dimorphism vectors for each species and performed a residual randomization to statistically evaluate difference in sexual shape dimorphism (see Hollander et al. 2006; Adams and Collyer 2007, 2009; Collyer and Adams 2007). We compared the observed difference in vector magnitudes with an empirically generated random distribution (from 9,999 iterations) obtained by permuting residuals from a reduced model that contained only main effects. For factorial designs, this procedure has superior statistical power to alternative randomization procedures (Anderson and ter Braak 2002).

To determine whether patterns of sexual shape dimorphism were consistent across localities within each species, we performed a MANOVA in which locality and sex were main effects, with a locality*sex interaction term. A separate MANOVA was performed on each species. Patterns of sexual shape dimorphism were then compared across localities, using the vector approach described above. Additionally, we performed a multivariate analysis of covariance with centroid size as a covariate and compared the fit of a model that incorporated size (species*sex*size) to a model without size (species*sex) (e.g., Gidaszewski et al. 2009) using Akaike's information criterion (AIC). All statistical analyses were performed in R (R Development Core Team 2008).

Finally, patterns of shape variation were graphically depicted in a principal component plot, with vectors of sexual shape dimorphism included. Thin-plate spline deformation grids were also generated for phenotypic means of males and females to facilitate biological interpretation of the observed shape differences within and between species.

RESULTS

No differences in bill curvature were identified between species or the sexes when we used the maxillary curvature index (Table 1A). By contrast, significant differences between species and the sexes were found with the mandibular index (Table 1B) and the circle-curvature index (Table 1C). With the latter approach, female Black-chinned Hummingbirds were predicted to have more curved bills than males ($K_{\text{males}} = 0.0043$, $K_{\text{females}} = 0.0053$), whereas this pattern was reversed in Ruby-throated Hummingbirds ($K_{\text{males}} = 0.0050$, $K_{\text{females}} = 0.0040$).

Using landmark-based morphometric methods, we identified bill-shape differences between species, between the sexes, and in the interaction between species and sex (Table 2A). The degree of sexual shape dimorphism thus differed between the species (Table 2B, C). Separate within-species analyses confirmed this finding, identifying significant sexual shape dimorphism in Ruby-throated Hummingbirds but not in Black-chinned Hummingbirds (Table 2B, C). Additionally, size did not explain this pattern, given that a model that included size as a covariate did not provide a better overall fit than the model that included species and sex alone ($\text{AIC}_{\text{species,sex}} = -138,574.4$ vs. $\text{AIC}_{\text{species,sex,size}} = -138,701.5$). Thus, allometric effects were relatively less influential on bill shape than the effects of species and sex.

Ruby-throated Hummingbirds exhibited a significant four-fold-greater degree of sexual shape dimorphism than Black-chinned Hummingbirds ($D_{\text{Ruby-throated}} = 0.0227$, $D_{\text{Black-chinned}} = 0.00521$, $P = 0.004$), a difference that was evident when viewed using PCA (Fig. 2). Further, visualization of bill shape with thin-plate spline deformation grids made these differences even more apparent (Fig. 2C). Specifically, the bills of Ruby-throated Hummingbirds were shorter, deeper, and stouter than the curved and elongated bills of Black-chinned Hummingbirds. And though the bills of Black-chinned Hummingbirds were relatively more

TABLE 1. Statistical results from linear measurements of (A) the maxillary curvature index, (B) the mandibular index, and (C) the circle-curvature method. Significant effects are shown in bold.

Source	Mean squares	Approximate <i>F</i>	df	<i>P</i>
(A) Maxillary curvature index: Arc:chord ratio				
Species	4.0 E-7	1.222	1 and 359	0.2902
Sex	2.3 E-5	0.02	1 and 359	0.8877
Species*sex	2.5 E-5	1.221	1 and 359	0.2698
(B) Mandible curvature index: height/gape				
Species	0.0033	33.6665	1 and 359	<0.0001
Sex	0.0014	14.7949	1 and 359	<0.0001
Species*sex	0.0001	0.0403	1 and 359	0.8409
(C) Circle-curvature: 1/radius				
Species	1.2 E-5	17.3115	1 and 359	<0.0001
Sex	3.0 E-5	6.6159	1 and 359	<0.0001
Species*sex	4.1 E-5	23.9225	1 and 359	<0.0001

TABLE 2. Statistical results from landmark-based geometric morphometrics quantifying (A) between-species morphological variation and (B, C) within-species morphological variation in Black-chinned Hummingbirds and Ruby-throated Hummingbirds. Significant effects are shown in bold.

Source	Pillai's trace	Approximate <i>F</i>	df	<i>P</i>
(A) Between species				
Species	0.6245	15.4193	35 and 325	<0.0001
Sex	0.1433	1.5576	35 and 325	0.0266
Species*sex	0.1491	1.6317	35 and 325	0.0161
(B) Within Black-chinned Hummingbirds				
Population	0.2018	1.7919	35 and 247	0.0059
Sex	0.1552	1.3019	35 and 247	0.1294
Population*sex	0.4425	0.0403	35 and 247	0.7083
(C) Within Ruby-throated Hummingbirds				
Population	1.3427	2.2764	35 and 38	<0.0001
Sex	0.6146	1.7313	70 and 78	0.0498
Population*sex	0.9122	0.9345	70 and 78	0.6123

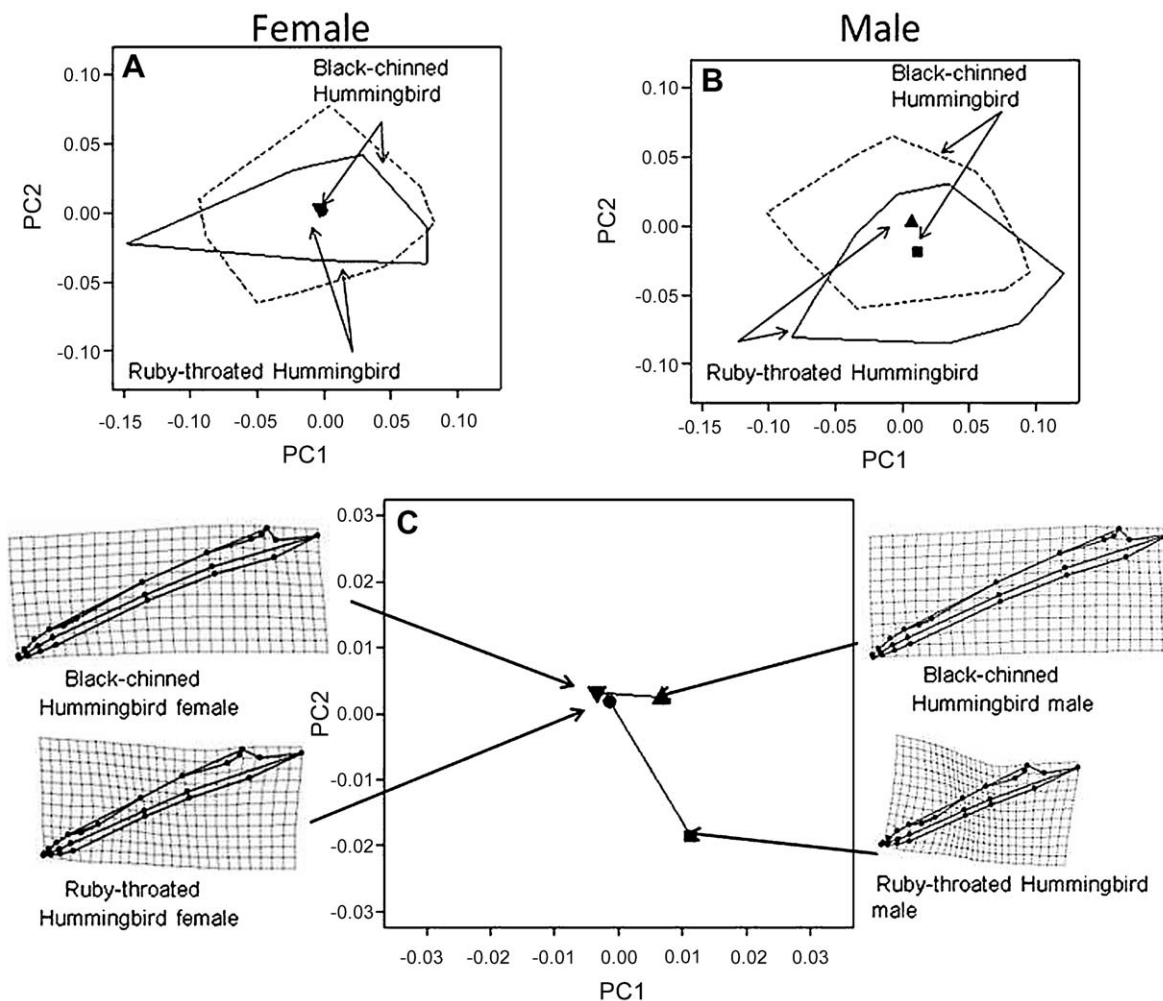


FIG. 2. Results of principal component analysis of all specimens (relative warp scores). Group means are displayed in each plot for the first two principal components (PC1 = 36.9% and PC2 = 22.9%, accounting for 59.8% of the overall shape variation). Convex hulls in PCA plot (A and B) are displayed with dashed lines to represent Black-chinned Hummingbirds, and solid hulls represent Ruby-throated Hummingbirds. (C) Thin-plate spline deformation grids are shown to visualize patterns of shape variation and have been accentuated by a factor of 3 to enhance interpretation.

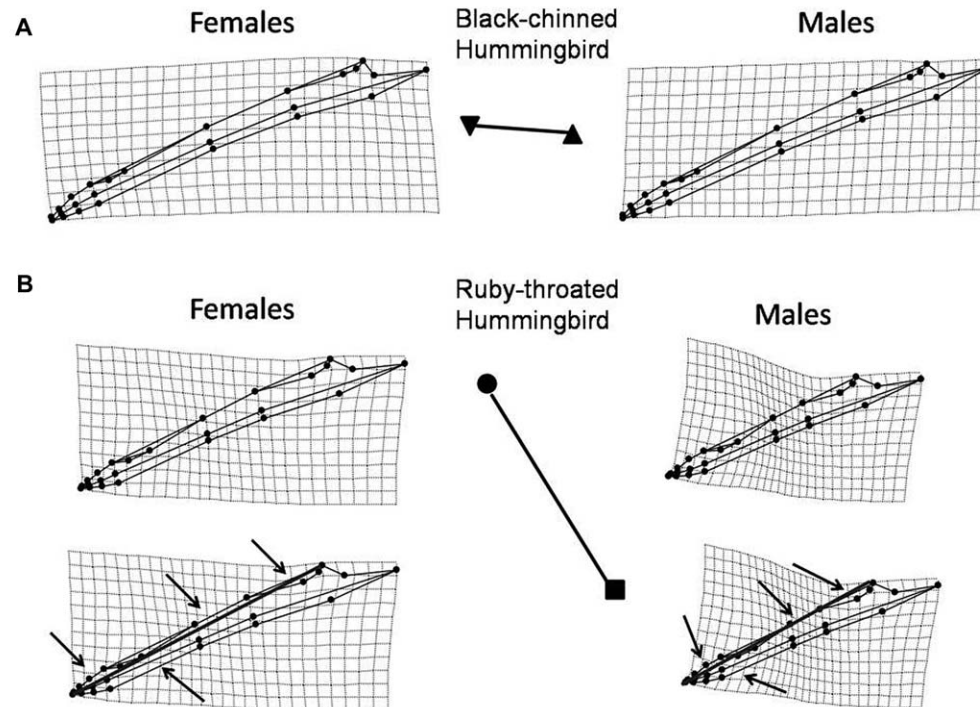


FIG. 3. Thin-plate spline deformation grids and magnitude of sexual shape dimorphism in (A) Black-chinned Hummingbirds and (B) Ruby-throated Hummingbirds. Arrows accentuate the patterns of bill shape in relation to the straight line drawn from the tip to the exposed culmen to accentuate specific shape differences between the sexes. Deformation grids are scaled to a factor of 3 to enhance interpretation.

curved than those of Ruby-throated Hummingbirds, both males and females in this species displayed similar bill shapes (Fig. 3A). By contrast, the significant sexual shape dimorphism in Ruby-throated Hummingbirds was such that bills of females were longer and more curved than the shorter and stouter bills of males (Fig. 3B). Interestingly, though the greater curvature in female Ruby-throated Hummingbirds is readily apparent in the graphic visualizations and is reflected in the landmark analyses, this pattern is not captured by the curvature index, which estimated females as having relatively less curvature in this species than males. We attribute this difference between patterns to the fact that bill curvature in this species is not constant across the length of the bill.

DISCUSSION

For over a century, biologists have examined patterns of sexual dimorphism and the possible mechanisms responsible for its evolution. In hummingbirds, sexual dimorphism in plumage, physiology, behavior, and bill size have been documented, and though some studies have demonstrated the importance of differences in bill curvature between the sexes, fewer studies have focused on sexual shape dimorphism. Here, we examined bill-shape differences between the temperate sister taxa Black-chinned and Ruby-throated hummingbirds and tested the hypothesis that patterns of sexual dimorphism in bill shape differed between these species. Using a maxillary curvature index, we detected no differences in bill morphology between species or sexes. By contrast, both a

mandibular curvature index and a circle-curvature approach revealed morphological differences between the two species and the sexes. When bill shape was quantified using landmark-based geometric morphometric methods, we found significant differences between species and identified significant differences in shape dimorphism between the sexes in Ruby-throated Hummingbirds but not in Black-chinned Hummingbirds. This latter result revealed that sexual shape dimorphism was species-specific.

One interesting finding of our study is that different measures of bill curvature produced divergent results. This is important, because it may cause researchers who employ alternative approaches to draw different conclusions from the same data. Some of these differences may be explained by the fact that these methods quantify different anatomical regions: one quantifies maxillary curvature whereas another quantifies mandible curvature. A third method assumes constant bill curvature, which is clearly not the case in the species examined here (Fig. 3). Landmark-based geometric methods are less constrained than the other methods and have proved capable of identifying shape differences in this and other systems. The fact that we found differences attributable to methodology should draw attention to the fact that some aspects of bill shape are not captured by the univariate curvature indices. We therefore recommend that future studies quantify bill shape using landmark-based geometric morphometric methods.

Another finding of our study is that closely related taxa can display differing degrees of sexual shape dimorphism. Why would we expect differences in sexual shape dimorphism among related taxa? One possible explanation is that bill shape is influenced by

sexual selection. The strength of sexual selection differs among species, and therefore the degree of dimorphism between the sexes might be expected to vary as well (Møller 1988, Andersson 1994, Owens and Hartley 1998). An alternative explanation is that sex-specific divergent selection occurs through differential responses to environmental gradients by each sex (Hendry et al. 2006). If such sex-specific responses differed among species, this process would result in varying degrees of sexual shape dimorphism as well. Finally, sexual dimorphism may be accentuated in species-poor communities, where members of each sex may inhabit ecological niches occupied by interspecific competitors in species-rich communities (Butler et al. 2007). Patterns consistent with this hypothesis have been identified in a number of vertebrate taxa (Schoener 1967, Dayan and Simberloff 1994) and may enhance the process of adaptive radiation in some circumstances, as sexes evolve different adaptations to resources and occupy different regions of niche space and morphospace (Butler et al. 2007).

Patterns of sexual shape dimorphism in bill shape are not unusual. In birds, it is relatively common for males and females of the same species to specialize on different trophic resources (Selander 1966), and in some species, sex-specific trophic differences are related to differences in bill morphology. For example, the tropical Purple-throated Carib exhibits bill-shape differences between the sexes that correspond to morphological differences in the *Heliconia* flowers that each sex primarily feeds on (Temeles et al. 2000, 2009; Temeles and Kress 2003). Sexual dimorphism in bill shape and resource use are also found in other avian species, such as the extinct *Huia* (*Heteralocha acutirostris*) of New Zealand (Burton 1974) and the African Green Woodhoopoe (*Phoeniculus purpureus*; Jamieson and Spencer 1996, Radford and du Plessis 2003), among others.

Although the reason(s) for the difference in sexual shape dimorphism in the two species that we studied is unclear, we hypothesize that differences in the breeding behavior of the two hummingbird species may be a contributing factor. Male and female Black-chinned Hummingbirds hold territories in different habitats, whereas male and female Ruby-throated Hummingbirds hold territories in the same habitat during the breeding season. It is likely that selection is strongest during the breeding period because it is the most energetically expensive time for hummingbirds: males exhibit costly courtship displays and territory defense (Stiles 1971, Armstrong 1987) and females must perform all parental care. We further hypothesize that the pattern of sexual shape dimorphism may also be attributable to "ecological release" (e.g., Selander 1966). Under this scenario, the lack of potential competitors in the breeding range of Ruby-throated Hummingbirds may allow expansion of its ecological niche that results in morphological differences between the sexes. In the Copper-rumped Hummingbird (*Amazilia tobaci*), for example, a broader feeding niche and greater morphological variation are observed in populations that co-occur with few other hummingbird species, whereas both ecological and morphological variation are reduced in populations that are sympatric with many other competing species (Feinsinger and Swann 1982). Our study reveals a similar pattern. The geographically isolated populations of Ruby-throated Hummingbirds (Robinson et al. 1996) display greater morphological differences between the sexes, whereas Black-chinned Hummingbirds display less morphological differentiation between the sexes and are found in communities that are sympatric with multiple hummingbird

species (Ewald and Bransfield 1987). Thus, differences in sexual shape dimorphism may be attributable to the interaction between intra- and interspecific competition in different communities (*sensu* Dayan and Simberloff 1994; see Butler et al. 2007). If this hypothesis is correct, we predict that other hummingbird species that are sympatric with Black-chinned Hummingbirds would also have reduced levels of sexual shape dimorphism compared with Ruby-throated Hummingbirds. We emphasize, however, that for these species, the biological causes of differential sexual shape dimorphism, such as variable community structure (Butler et al. 2007), sexual selection (Møller 1988, Andersson 1994), and differential responses to environmental gradients (Hendry et al. 2006), have yet to be fully explored.

We found that female Ruby-throated Hummingbirds have longer and more curved bills than males, although this is less dramatic than in Purple-throated Caribs (Temeles et al. 2000, 2005, 2009; Temeles and Kress 2003). Studies of the two species thus support Brown and Kodric-Brown's (1979) prediction that sexual differences in bill morphology should be greater in tropical than in temperate hummingbird species. Greater difference in the magnitude of sexual shape dimorphism in tropical than in temperate hummingbird species may be attributable to the widely distributed and morphologically similar flower resources that are available to temperate hummingbirds. The much greater diversity of floral species and floral forms in the tropics (Grant and Grant 1968) must surely contribute to greater shape variation at low latitudes. Examination of the difference in the magnitude of sexual shape dimorphism in a wider array of taxa will make it possible to address how patterns of sexual shape dimorphism evolve across the landscape and to evaluate the extent to which sexual shape dimorphism is associated with the environmental niche of each species. When viewed in a broader context, ecological examinations of sexual shape dimorphism must also be viewed in light of phylogenetic history to fully understand the interplay between bill-shape sexual dimorphism and resource use and the coevolution of these two suites of traits.

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APPENDIX

Specimens used to quantify morphological variation in Black-chinned Hummingbird and Ruby-throated Hummingbird. We examined the left lateral side of bills from collections at Carnegie Museum of Natural History (CMNH), Cornell University Museum of Vertebrates (CUMV), Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), Los Angeles County Museum (LACM), Museum of Comparative Zoology (MCZ), Museum of Southwestern Biology (MSB), Museum of Vertebrate Zoology (MVZ), San Diego Natural History Museum (SDNHM), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History (NMNH), Western Foundation of Vertebrate Zoology (WVZ), and Yale Peabody Museum (YPM). Specific specimens, listed by institution, include the following.

CMNH: 125705, 125706, 125710, 141875, 142477, 151407, 152912, 153151, 153802, 154036, 154146, 154621, 158828, 1588289, 158830, 158831, 158832, 158833, 158834, 158836, 158837, 159323, 159324, 159325, 159327, 159328, 159329, 159330, 159331, 159332, 159333, 159334, 159335, 159336, 159337, 159338, 159339, 159340, 159342, 159343, 159345, 159346, 159347, 159348, 159349, 159350, 166922, 167457, 168761, 169649, 170846, 170867, 95217.

CUMV: 14986, 21604, 23717, 24397, 37009, 44079, 44128, 44129, 44130, 44131, 44171, 49013, 50001, 50780, 51239, 5352, 5355, 5357, 5358, 5361, 5362, 5363, 5364, 5365, 5367, 5382.

DMNH: 1400, 1426, 1436, 19019, 19025, 59806.

FMNH: 138705, 138720, 138723, 138725, 14653, 14654, 14655, 14656, 14657, 14658, 14659, 14661, 14662, 14663, 14666, 14667, 14668, 14670, 14672, 14673, 14674, 14675, 14676, 14678, 159838, 159839, 161019, 16575, 16576, 93036, 93037, 93038, 93039, 93040.

LACM: 14127, 14138, 14139, 1927, 3381, 78618, 78619, 78621, 78623, 78624, 78625, 78626, 78627, 78632, 78643, 78646, 78652, 78653, 78654, 78656, 78659, 78661, 78662, 78663, 78664, 78668, 78669, 78671, 78677, 78678, 78683, 78684, 78688, 78691, 78694.

MCZ: 100182, 103286.

MSB: 14801, 22663, 22665, 22668, 22670, 22671, 22677.

MVZ: 107024, 116741, 121811, 19920, 19921, 19922, 19923, 19925, 22484, 22704, 26729, 26730, 27927, 27928, 27929, 27930, 27931, 3192, 3194, 3197, 32864, 32870, 32875, 32878, 32880, 32881, 32882, 32883, 32884, 32887, 32888, 32889, 32900, 32903, 3655, 3698, 3700, 3785, 40727, 40728, 40731, 41534, 41927, 4194, 4195, 43242, 45343, 5249, 77338, 80946.

NMNH: 108369, 117258, 117269, 129247, 129249, 129250, 129252, 129257, 134343, 140254, 140255, 140256, 140257, 140258, 140259, 140266, 168422, 203268, 234334, 235077, 235074, 258387, 467031, 589963, 91738, 91740, 94957, 91959.

SDNHM: 17251, 22386, 22387, 22389, 22463, 30108, 30417, 449, 450.

UMMZ: 111820, 113646, 113649, 126291, 126292, 126294, 126295, 126296, 126297, 126299, 126300, 126301, 126301, 126302, 126303, 126304, 126306, 126307, 126310, 126314, 134697, 136434, 156250, 164455, 164461, 164463, 164468, 164470, 164471, 164472, 164473, 164474, 164490, 164491, 164492, 164492, 164496, 164498, 164500, 164501, 164502, 164504, 164505, 164506, 164507, 164508, 164509, 164510, 164514, 164515, 164517, 164518, 164519, 164525, 164526, 164527, 164528, 164529, 164530, 199030, 199031, 213109, 213110, 221599, 221794, 224043, 231028, 231029, 236468, 238200, 239425, 239499, 239601, 239604, 239631, 240778, 240967, 241265, 241283, 31639, 52980, 55809, 62710, 62711, 62713, 62714, 67020, 71337, 74542, 90352.

WVZ: 10119, 1515, 1516, 1517, 21798, 21803, 21804, 21806, 21809, 2714, 32155, 32156, 49304, 49308.

YPM: 6442, 99650.